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Quantifying the impact of vegetation-based metrics on species persistence when choosing offsets for habitat destruction

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Running head: Quantifying biodiversity offset metrics

Impact statement: This study highlights the importance of using offset metrics which account for the impacts of development on long-term species persistence.

Key Words: biodiversity offsets, biodiversity metrics, population viability analysis, simulation tool, species persistence

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Abstract

Developers are often required by law to offset environmental impacts through targeted conservation actions. Most offset policies specify metrics for calculating offset requirements, usually by assessing vegetation condition. Despite widespread use, there is little evidence to support the effectiveness of vegetation-based metrics for ensuring biodiversity persistence. We compared long-term impacts of biodiversity offsetting using area only; vegetation condition only; area x species' habitat suitability; and condition x species' habitat suitability in development and restoration simulations for the Hunter Region of New South Wales, Australia. We simulated development and subsequent offsetting through restoration within a virtual landscape, linking simulations to population viability models for three species. Habitat gains did not ensure species persistence. No net loss was achieved when performance of offsetting was assessed in terms of amount of habitat restored, but not when outcomes were assessed in terms of persistence. Maintenance of persistence occurred more often when impacts were avoided, giving further support to better enforce the avoidance stage of the mitigation hierarchy. When development affected areas of high habitat quality for species, persistence could not be guaranteed. Therefore, species must be more explicitly accounted for in offsets, rather than just vegetation or habitat alone. Declines due to a failure to account directly for species population dynamics and connectivity overshadowed the benefits delivered by producing large areas of high-quality habitat. Our modelling framework showed that the benefits delivered by offsets are species-specific, and simple vegetation-based metrics can give misguided impressions on how well biodiversity offsets achieve no net loss.

Introduction

Biodiversity offsetting is used around the globe to deliver conservation actions aimed at achieving no net loss or net gain of biodiversity to compensate for impacts caused by development (Bull et al. 2016a). However, lack of consistency in offsetting policies at different levels of governance (e.g., state versus federal) and different stages of offset implementation make it difficult to consistently define what achieving no net loss requires (Maron et al. 2018). Moreover, it is unclear whether offsets achieve their claimed conservation outcomes under current frameworks (zu Ermgassen et al. 2019). The ineffectiveness of biodiversity offsets can be attributed to inconsistent and unclear biodiversity metrics (Gibbons et al. 2018) and inadequate post-implementation monitoring and compliance at offset sites (Theis et al. 2019). Accurately measuring biodiversity is challenging, and popular offsetting metrics assign habitat condition or area scores to a site by assessing, scoring, and weighting several vegetation attributes (Oliver et al. 2014; zu Ermgassen et al. 2019). With habitat condition scores varying across an area of impact, it is common to simply sum scores such that, for example, 25 hectares of perfect-condition vegetation would receive the same overall offset score as 50 hectares of vegetation that scores 50% less (Chapter one and two). Reliance on habitat- and vegetation-based offsetting metrics (Gibbons et al. 2018) can be problematic when such metrics do not strongly correlate with the ecological features that an offsetting program seeks to conserve (Kujala et al. 2015a). Often, habitat attributes and vegetation-based surrogates fail to capture the extent of biodiversity that is claimed (Cristescu et al. 2013; Hanford et al. 2016). Moreover, current offsetting metrics are likely to result in undervaluation of degraded or smaller patches, even when these are of high ecological importance (Wintle et al. 2019).

The premise of many offset policies is to ensure persistence of populations, species, ecosystems, and communities (Maron et al. 2012). However, this goal is not currently supported by relevant metrics. No net loss policies require that offset sites deliver the same or higher vegetation-condition scores relative to impact sites but achieving this target alone may not ensure sites will deliver long-term

benefits or ensure persistence of populations or species (Gardner et al. 2013). Therefore, assessment of the ability of vegetation condition to act as a surrogate for species persistence appears to be a necessary first step in offset-policy evaluation. Combining vegetation condition measures with explicit species assessments in an adaptive management framework can be an effective approach to offset management (Drielsma et al. 2016). However, there has been little quantitative research on how vegetation-based offset metrics truly function in relation to species-persistence targets (Gelcich et al. 2017). To address this gap, we developed a simulation framework to compare performance of commonly used vegetation-based offset metrics with alternative metrics that include more detailed species data. Our framework combines a model simulating development and offsetting with population viability analyses (PVAs) for three species in the Hunter Region, New South Wales (NSW), Australia.

Methods

Study region and target species

The Hunter Region in NSW, Australia (Figure 1), has a long history of agriculture and coal mining, with mine leases and applications covering around 21% of the Hunter Valley (90,500 ha; Kujala, Whitehead, Morris, et al., 2015; Kujala, Whitehead, & Wintle, 2015). This region is home to several susceptible species, including the three we considered here: squirrel gliders (*Petaurus norfolcensis*), Powerful Owls (*Ninox strenua*), and northern brown bandicoots (*Isoodon macrourus*). Squirrel gliders are hollow nesting, gliding marsupials widely distributed along the east coast of Australia (Sharpe & Goldingjay 2017). The Powerful Owl is a large owl with a wide home range in southeastern Australia (Soderquist & Gibbons 2007). Both species are considered vulnerable in NSW. Northern brown bandicoots are medium-sized ground-dwelling marsupials with short life cycles, high population growth rates, and moderate dispersal (Ramalho et al. 2018). This species is not currently considered threatened. The species examined here were selected primarily because they are sufficiently well studied to build spatially explicit population models.

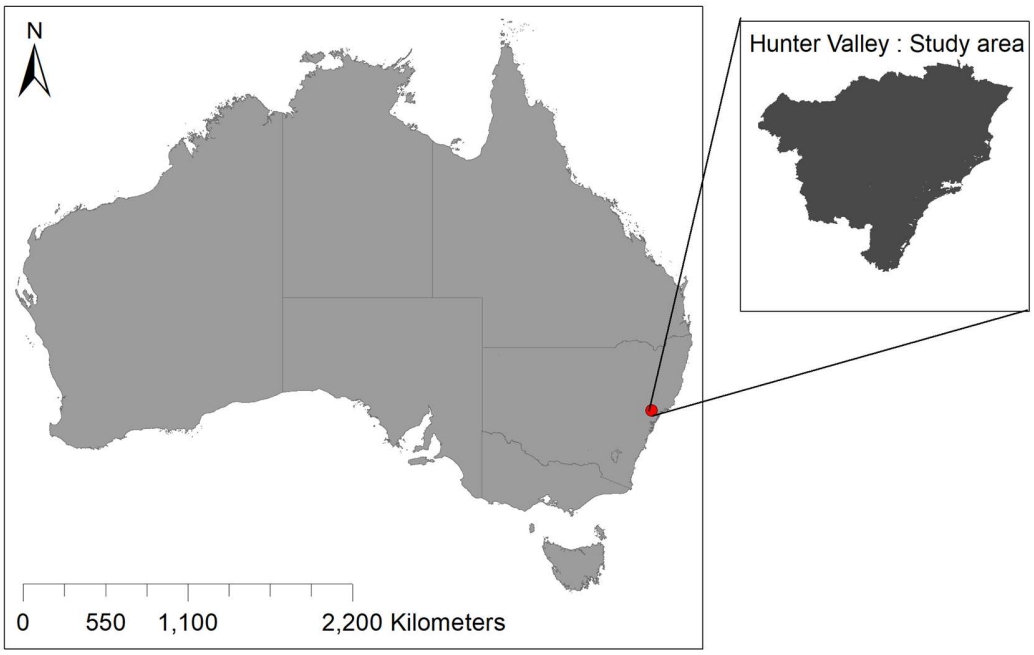

Figure 1: *Hunter Valley region, New South Wales, Australia.*

Habitat and species data

We used two types of raster maps to conduct our simulations: a vegetation condition map and species habitat suitability maps (Kujala et al. 2015a). The vegetation-condition map was used to estimate the native vegetation condition for the Hunter Region at 100-m grid-cell resolution. Scores ranged from zero to one, depending on known land-use categories. Zero indicates areas containing no natural vegetation, whereas 0.5 could indicate agricultural land with remnant vegetation. One indicates extant and relatively undisturbed vegetation (Figure S.1). Species distribution models (SDMs; 100-m grid-cell resolution) were built for each species in *MaxEnt* (Elith et al. 2011), with values of zero to one (Figure S.2).

Being based on presence-only data, the SDMs represent only relative habitat suitability for each species (Guillera-Arroita et al. 2015). We interpreted *MaxEnt's* logistic output values as roughly indicative of carrying capacity (Merow et al. 2013), giving the fraction of maximum carrying capacity attainable for each species (Appendix S4.2). Because *MaxEnt* outputs are not comparable between

species, we examined relative changes in total habitat suitability between scenarios only within species.

We multiplied our vegetation condition layer and SDMs to produce a proxy of current habitat suitability (Figure S.3) for each species; values ranged from zero to one. The resulting habitat suitability map for each species represented the baseline used to compute the impacts of each development and its required offset. This was also the baseline map used to define landscape structure and determine carrying capacity in our spatially explicit PVAs.

Modelling framework

We used the above raster layers as inputs to simulate development impacts and calculate offset requirements within R version 3.6 (The R Foundation for Statistical Computing 2017). For all development and offset simulations, we used our current habitat suitability map as a baseline for each species. Each subsequent raster generated by the simulations was then used to represent habitat changes within the PVAs for each species.

Our modelling framework involved five steps: 1) simulate developments; 2) calculate offset requirements; 3) restore vegetation until offset requirements are met; 4) construct a landscape patch structure for the species; and 5) build population models for the species to predict population persistence (Figure 2). We assumed across all metrics that restoration returns vegetation condition to the highest level immediately. Because we were interested in comparing relative performance of offset metrics, rather than providing realistic predictions about restoration success, it was deemed unnecessary to perfectly characterize variation in restoration outcomes. We acknowledge this is a coarse simplification of likely success of restoration efforts (Maron et al. 2012).

Development impacts

We simulated four development scenarios for each species: 1) S1, large developments with strict avoidance of high-quality habitats; 2) S2, large targeted developments which removed high quality

habitat; 3) S3, small developments with strict avoidance; and 4) S4, small targeted developments. All four scenarios had a total development footprint of 100,000 hectares (approximately 21% of the landscape). Large developments were each 10,000 hectares and occurred ten times in the landscape during one simulation (S1, S2). Small developments were 1,000 hectares and occurred 100 times (S3 and S4). Scenario one and three represented our strict avoidance scenarios, where development was targeted toward the least suitable habitat for each species, based on species current habitat suitability**.** This aligns with the avoidance stage of the mitigation hierarchy (Phalan et al., 2017). In targeted development scenarios S2 and S4, development was directed to high suitability areas to represent a worst-case scenario. We also simulated two additional development scenarios where impacts were allocated randomly (Figure S.4, S.11, S.12). Each scenario was repeated 50 times to account for spatial stochasticity. Development impacts reduced vegetation condition of affected grid cells to zero.

Offset metrics and simulation

We calculated offset exchanges based on area only (area), vegetation condition only (condition), area x habitat suitability (areaXSDM), and condition x habitat suitability (conditionXSDM). Area was based solely on the area lost due to development, and the offset simply restored the same area of habitat elsewhere. Condition was calculated by summing the current habitat condition lost due to development, and restoration was required to enhance habitat condition by an equivalent amount elsewhere. The metric areaXSDM, as with area, was based on the area lost due to development but differed in that offsets were restricted to an equivalent area in the landscape that was also suitable habitat for the species as modelled by the SDM (after applying a species-specific threshold to differentiate between habitat and non-habitat; Table S.1). The metric conditionXSDM as with condition, offset the summed current habitat condition lost due to development but restoration was again restricted to species' habitat as modelled by the SDM (Figure S.5).

These metrics were intended as coarse simplifications of offset metrics currently used in Australia. In New South Wales, offset legislation relies on the biodiversity assessment method (BAM) which

incorporates 30 measures of habitat and landscape to assess biodiversity (NSW Office of Environment and Heritage, 2018). These are largely focused on habitat features. When species are accounted for in the BAM metric, measurements generally include species presence or absence and habitat suitability. These are measures accounted for in the above metrics, albeit simplistically. We used a multiplier of two for all offset targets, meaning that offsets needed to deliver gains of twice the amount lost. Large multipliers (e.g., greater than ten) are more likely to ensure no net loss; however, relatively low multipliers (e.g. two to three) are commonly used in practice (Bull et al., 2016b; Laitila et al., 2014). Multipliers in the BAM vary between one and three and depend on species' sensitivity to loss and to offset gains. Therefore, the multiplier of two we used accounts for a moderate-to-high sensitivity to loss and a moderate-to-high potential gain (NSW Office of Environment and Heritage, 2018).

For all repetitions of our development scenarios, we restored impacts based on all four metrics. A starting point for restoration was randomly selected within a buffer zone around the development (Appendix S2). Each cell adjacent to the starting point was searched and restored until the total offset requirement was met. At the end of each simulation an updated raster layer was generated with the simulated developments and offsets added to the species current habitat suitability layer.

Population Viability Analysis (PVA)

Population viability analyses estimate the probability of a species persisting in a landscape given its habitat requirements, dispersal ability, and demographic variables. We built spatially explicit PVAs for each species with the software RAMAS GIS 5.1 (Akçakaya & Root 2005). We used the current habitat suitability maps of the species to develop the baseline patch structure and to simulate population dynamics over a 100-year period prior to developments or offsets. Patch structure is delineated by RAMAS with a habitat suitability threshold and species-specific information on dispersal (Akçakaya, 2000; Akçakaya & Root, 2005; Figure 2). We used species-specific maximum training sensitivity plus specificity (Cardador et al. 2018) as our threshold values, which were

extracted from the *MaxEnt* model outputs (Table S.1). We derived species-specific dispersal and demographic parameters from the literature and tested them through sensitivity analyses (Table S.1**;** Figure S.7). We then re-ran the PVAs for each species, replacing the baseline patch structures with those generated from development and offset simulations.

Scenario analyses

We ran 50 simulations per development scenario and 50 corresponding restorations for each metric, for all three species, for which PVAs were run across 1000 replicates over 100 years. We used two measures to evaluate metric effectiveness: percent change in total habitat suitability from baseline, calculated using the species' updated raster maps, and percent change in average estimated minimum abundance (EMA) from baseline, calculated from the PVAs. Estimated minimum abundance is the smallest population size that occurs across the duration of a simulation averaged across replicates (Wintle, 2013). We examined confidence around the 50 repeats to assess correlations between metric use and changes in habitat suitability and EMA from baseline. We also assessed changes in landscape structure by comparing mean number and size of suitable habitat patches in the landscape with minimum and maximum EMA values (Appendix S5).

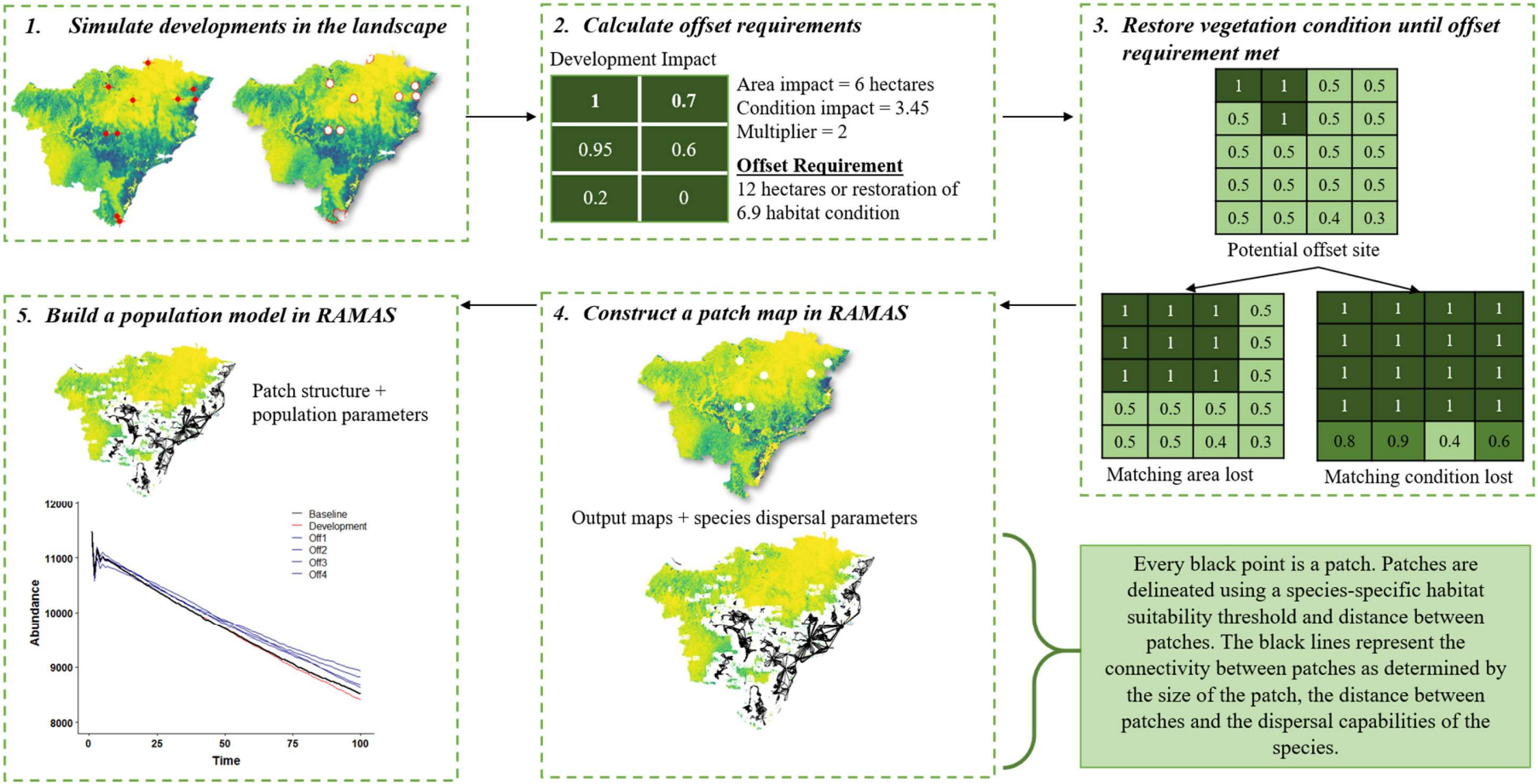

Figure 2: *Simulation modeling framework conducted within R (steps 1 to 3) and RAMAS GIS (steps 4 and 5). The maps represent habitat suitability on a scale of zero to one (yellow, not suitable; blue, highest quality habitat; green squares in steps 2 and 3, show grid cells in the landscape and their condition values; red points in step 1 show development sites chosen; white circles in step 1 show sites cleared). The impacts of each development are calculated in terms of area and condition lost (step 2). Vegetation condition is restored until the requirement is met either in terms of area or condition (step 3). Each resulting map, including development without offsets and developments with offsets, is used in RAMAS GIS to build a patch map based on the resulting landscape structure and species dispersal parameters (step 4). The patch map is used in a spatially explicit population model that tracks abundance of the species through time (step 5).*

Results

Change in habitat suitability

Development impacts

Impacts of development on the percent change in habitat suitability were consistent across species but varied between scenarios. Targeting developments to species' high-quality habitat (S2 and S4) caused a 10.5% (± 1SD 0.8%) decline in habitat suitability for our species (Figure 3), whereas under strict avoidance (S1 and S3) species lost on average 1.7% (±1SD 0.5%) of their habitat (Figure 3).

Offset metrics

The effectiveness of offset metrics in compensating for development impacts on habitat varied among development scenarios and species. The area-only approach consistently failed to achieve no net loss of habitat suitability for all scenarios and species (Figure 3). Thus, simply compensating for the area lost did not produce enough habitat to match development impacts. Under the avoidance scenarios (S1 and S3), the three remaining metrics achieved net gains in habitat suitability for all species (Figure 3). However, when developments were targeted (S2 and S4), the benefits delivered by most metrics – except conditionXSDM – were smaller. The areaXSDM metric failed to achieve no net loss for the Powerful Owl and northern brown bandicoot in S2 and for all three species in S4. This is likely because in high-impact development scenarios, even when offsets are targeted towards high suitability pixels (e.g. areaXSDM), simply matching area alone will not compensate for enough of the lost condition to return the overall habitat suitability back to the species baseline level.

The conditionXSDM metric produced net gains in all four development scenarios across all three species. Notably, when using the conditionXSDM metric, because offset requirements were high, around 24% and 28% of offset requirements respectively for the Powerful Owl and northern brown bandicoot, were not met. In these scenarios the simulation ran out of habitat to restore and still resulted in large net gains in habitat suitability compared to baseline.

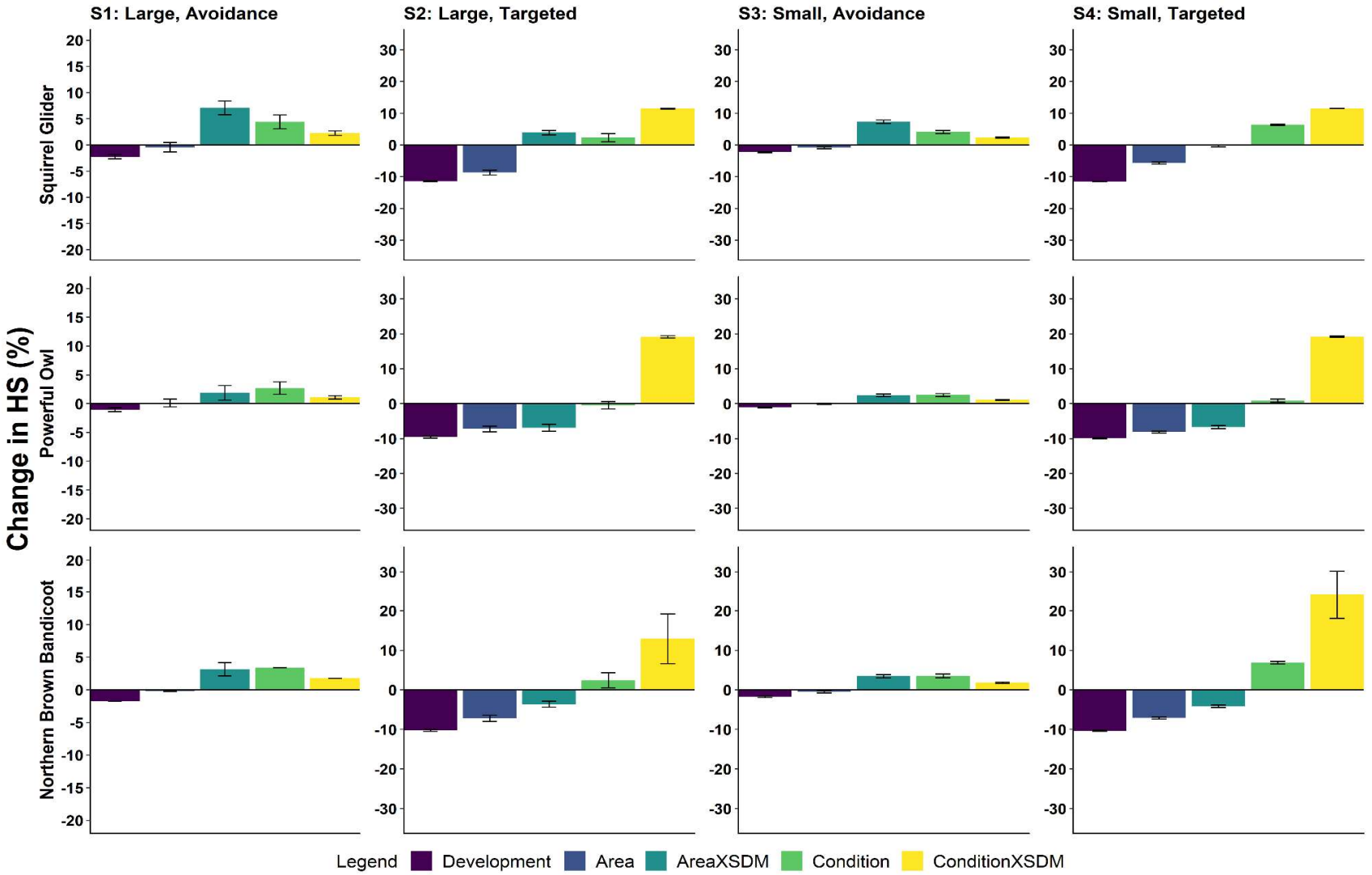

Figure 3: *Percent change in habitat suitability (HS) from baseline for three species under four development scenarios (S1, large development avoidance; S2, large targeted development; S3, small development avoidance; S4, small targeted development). Error bars show SD [generated from 50 repetitions for each simulation; dark blue, the development impact; blue, area only; turquoise, area x habitat suitability [SDM]; green, condition only; yellow, condition x habitat suitability [SDM]).*

The condition-only approach also achieved no net loss and sometimes net gains in habitat suitability for all species and scenarios; however, gains were smaller than the conditionXSDM metric (Figure 3). Compensating for condition, particularly when coupled with information on SDMs, resulted in larger offset areas than area-based metrics (Table S.2). For all species the conditionXSDM metric resulted on average in patches 1.4 times larger than the other three metrics and 1.7 times larger than the species baselines patch structure (Figure 5).

Change in Estimated Minimum Abundance (EMA)

Development impacts

Development impacts on EMA were not proportional to the benefits observed on habitat suitability and varied among species and scenarios (Figure 4). Declines in EMA were less dramatic when the size of the development was small (S3, S4; Figure 4), except for the Powerful Owl, for which highest declines were observed under S4. Development impacts on squirrel glider EMA were higher than the other two species, particularly when the developments were targeted (S2, S4; Figure 4). Under all four development scenarios, changes in northern brown bandicoot EMA were minimal and even showed a small net gain in S4 (Figure 4). This could be due to the high reproduction rates of northern brown bandicoots and the influence of development on the landscape structure, which may have been more favourable for this species.

Offset Metrics

Benefits delivered to population persistence by offsets varied notably among metrics, species and scenarios; generally, most of the metrics failed to achieve net gains. In our worst-case scenarios, S2 and S4, no net loss in EMA was only rarely achieved, and only when using area only and areaXSDM in some repeats (Figure 4). Generally, all three species' abundances declined significantly across all metrics in S2 and S4 even when the metrics resulted in significant gains in habitat suitability (e.g. conditionXSDM; Figure 3).

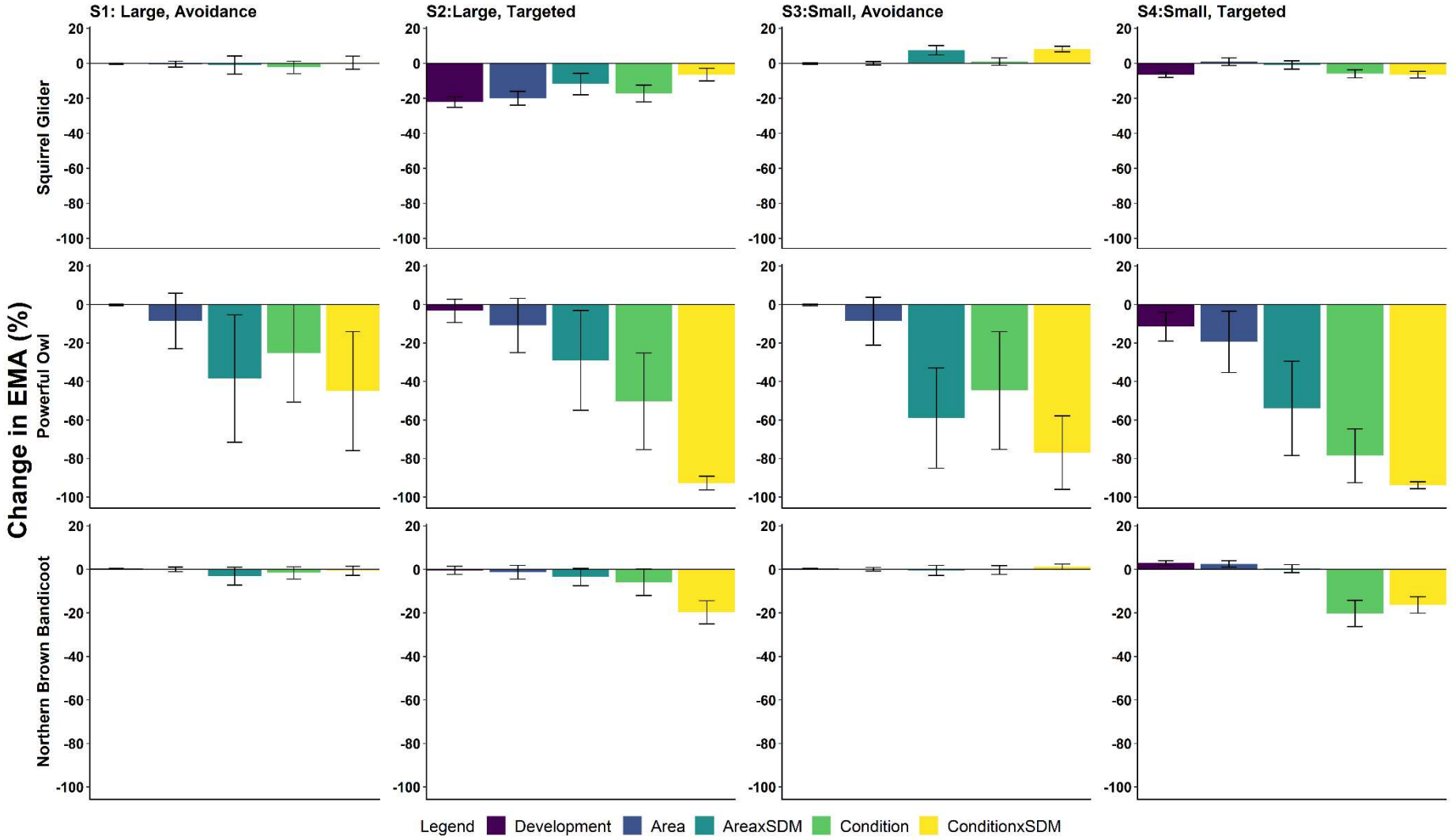

Figure 4: *Percent change in estimated minimum abundance (EMA; averaged across population viability assessments) from the species baseline for three species under four development scenarios (error bars, SD in EMA produced by the simulation runs; S1, large development avoidance; S2, large targeted development; S3, small development avoidance; S4, small targeted development; dark blue, the development impact; blue area only; turquoise, area x habitat suitability [SDM]; green, condition only ; yellow, condition x habitat suitability).*

Development impacts on squirrel glider EMA were best offset when using metrics that included species-specific information on habitat suitability (SDM; Figure 4). When development impacts were small and a strict avoidance approach was taken, the two SDM inclusive metrics achieved net gains for the squirrel glider. Comparatively, no net loss of EMA for Powerful Owls was only achieved in some simulations, generally when using the area metric (Figure 4), even though this metric failed to achieve a no net loss in habitat suitability (Figure 3). Similarly, not net loss was achieved for northern brown bandicoots in some replicates when using the two area-based metrics (Figure 4). Condition-based approaches only resulted in no net loss for northern brown bandicoots in some simulations when the development impacts were untargeted (S1 and S3; Figure 4). Across all three species, the conditionXSDM metric, which produced the largest gains in habitat suitability, frequently failed to compensate for declines in EMA. In Powerful Owls and northern brown bandicoots, the use of this metric resulted in larger declines than development on its own (Figure 4).

Landscape configuration and population declines

Scenarios that resulted in more patches, generally resulted in higher EMA values for all species (Figure 5). The largest declines in EMA occurred when the development or offsets reduced the number of patches available in the landscape. Furthermore, across all species, EMA was highest when patch size was small, although this relationship was not as clear for the squirrel glider (Figure 5). It appears that in scenarios where patch size was large (e.g., conditionXSDM metric; Table S.2) there was a corresponding decline in the number of patches available and overall lower EMA values relative to the species' baselines. This is clear in northern brown bandicoots and Powerful Owls for which conditionXSDM produced very large patches with fewer patches available overall (Figure 5). This suggests that, at least for these species, producing large, continuous offset patches may not ensure population persistence. Instead, scenarios that resulted in maintaining multiple patches had overall the highest EMA (Figure 5).

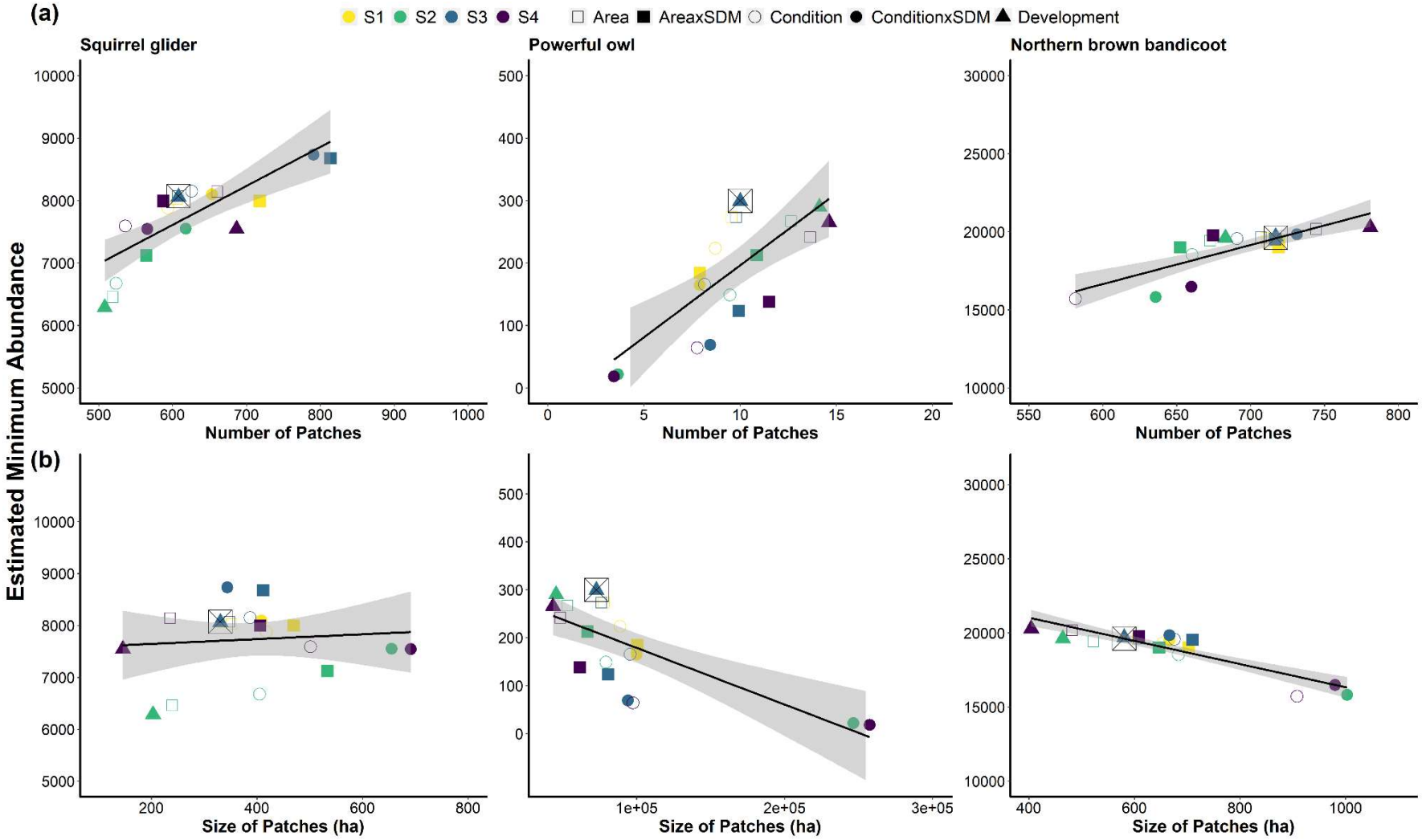

Figure 5: *Comparison of the estimated minimum abundance (EMA) values with average (a) number of patches and (b) size of patches under four development scenarios (yellow, S1, large development avoidance; green, S2, large targeted development; blue, S3, small development avoidance; dark blue, S4, small targeted development) and 4 metrics (open square, area; solid square, area x habitat suitability [SDM]; open circle, habitat condition; solid circle, condition x habitat suitability [SDM], and solid triangle, development; black square with a cross, baseline value for number of patches relative to EMA; trend line, relationship between EMA and number or size of the patches as a linear regression; gray shading, variation around regression estimate).*

Discussion

We quantitatively demonstrated how habitat loss and mitigation of these losses translates to species persistence. When performance of offsetting was measured in terms of total habitat gains, achieving no net loss, and even net gains was feasible with the metrics we tested. This was particularly apparent when information on a species' habitat suitability was included in offset calculations. In all four development scenarios, metrics that accounted for SDM values delivered the highest net gains in total habitat suitability (Figure 3). This may be important when developments are likely to affect core habitats and therefore require offsets to be strategically assigned to areas of high quality (Gordon et al. 2011). Conversely, offset trades based solely on area lost versus area gained failed in all cases to deliver a no net loss in habitat suitability for all three species (Figure 3). Thus, simply accounting for area resulted in offsets that were too small to match development impacts in terms of lost habitat value. This is consistent with previous research showing that offset trades based on area only metrics are unlikely to achieve no net loss, particularly without significant multipliers (Bull et al. 2016b; Sonter et al. 2019).

Despite significant gains in habitat suitability, none of the metrics were consistently effective at offsetting development impacts on species' populations (Figure 4). Our results highlight that relying on vegetation condition, or even changes in habitat suitability for target species, as a measure of offset success can be misleading. This was apparent in the vastly different outcomes we observed between habitat suitability and EMA (Figure 3; Figure 4). Depending solely on habitat suitability could result in the false interpretation that offset actions are having long-term benefits for the target species. This could lead to exacerbated species declines and nudge species of least conservation concern towards a declining trajectory, even when every offset requirement is being met (Maron et al. 2015). This is also consistent with previous research demonstrating that restoration actions based on vegetation metrics alone do not effectively capture target species or populations (Cristescu et al. 2013; Hanford et al. 2016).

We also demonstrated the difficulty in achieving no net loss at a landscape scale (Peterson et al. 2018). Even when each individual offset action delivers a no net loss, this may not result in a landscape level benefit for the species. The metrics we tested all failed to support the structural and functional landscape characteristics necessary for the three species (Figure 5). Although basic landscape metrics, such as patch size and distance, are usually incorporated into offset metrics (Gibbons et al. 2016), these basic structural connectivity measures still largely fail to capture development impacts on species or populations (Crouzeilles et al. 2015). There are benefits to accounting for functional connectivity in the planning stages of offsets, at least in terms of achieving no net loss targets (Bergès et al. 2020). Our results showed that the negative impacts of using only habitat-based metrics and ignoring species-specific connectivity may be significant, vary greatly among metrics, and, most alarmingly, are likely to go unnoticed unless changes in population dynamics are tested explicitly. These findings provide strong support for earlier calls that both structural (e.g. patch size and distance) and functional connectivity metrics (e.g. metapopulation connectivity and capacity; Bojkovic, Petrovic, Boz, & Anic, 2015; Moilanen et al., 2005) should be accounted for in the early stages of impact assessment and offset planning to avoid unexpected declines in populations and species (Tarabon et al. 2019a, 2019b).

This case study is a simplified version of current offset procedures, and we applied it to only three species. Commonly, practitioners seek to design offsets to provide benefits for multiple target species simultaneously. We focused only on single-species outcomes to keep comparisons between metrics as transparent as possible. However, these results are naturally further complicated when considering how metric choice could interact with multiple species priorities (Whitehead et al. 2017). Exhaustive collection of data on the ecology and demographic processes driving persistence is not possible for all species (Birkeland & Knight-lenihan 2016). However, increased availability of abundance and demographic data may fill this information gap over time. Failing to capture complex processes that drive changes in population persistence at a landscape level is likely to exacerbate biodiversity declines, such as those observed here (Maron et al. 2016). Assessing species-specific metrics, such as abundance or density, that

are generally driven by ecosystem processes (Otto et al. 2014), alongside vegetation condition metrics, may better enable offsets to capture the key species managers are aiming to protect and ensure long-term population persistence (McKenney & Kiesecker 2010; Schmeller et al. 2017). Inclusion of these data in offset approaches would likely improve offset outcomes for rare, low-density species with large home ranges, such as the Powerful Owl. Similarly, our use of habitat suitability information here, though largely ineffective at accounting for population persistence, did demonstrate benefits for delivering habitat gains in comparison to area or condition only metrics. For example, the net gains in habitat suitability delivered using the conditionXSDM metric resulted in some success for the squirrel glider populations so long as impacts were avoided where possible and ideally small (Figure 4).

Recent shifts in policy requirements have promoted using habitat suitability information where possible and additional information on populations and abundance when required (Queensland Government 2014; NSW Office of Environment and Heritage 2018). Our use of species-specific habitat suitability was an attempt to reflect rapidly changing offset policies and increased interest in incorporating more species-specific information into offset calculations (Moilanen & Kotiaho 2018). Although SDMs do not capture population-level processes (Kujala et al. 2018), they provide a more accurate description of habitat suitability than simple vegetation-based metrics (Guisan & Thuiller 2005). Data required to build SDMs are becoming more prevalent and are relatively easy to access and collate at large scales (Boykin et al. 2012). Use of SDMs within biodiversity offsetting may also provide developers with information necessary to avoid areas where biodiversity impacts are likely to be significant (Houdet & Chikozho 2014). Moreover, SDMs can explicitly target restoration efforts towards areas where habitat gains will be largest (Whitehead et al. 2017).

It is likely there is no single way of overcoming the challenges associated with offsetting for every scenario and species. Based on our results, four key conclusions and recommendations follow for offset policies. First, and reinforcing earlier calls (Phalan et al. 2017; Sonter et al. 2020), avoidance of impacts through careful placement of new development is the most effective way of ensuring species persistence is

maintained. Given challenges associated with increasing complexity in current offsetting metrics and the fact that some developments are not offsetable, avoiding and minimizing negative development impacts where possible is essential. Second, when developments affect areas of high suitability for species, it is essential that species, not only their habitat, be explicitly accounted for in offsets. We observed very different conservation outcomes when comparing habitat gains and species persistence. Ensuring the metrics accurately reflect the values we aim to conserve is crucial (Cristescu et al. 2013). This is further dependent on policy frameworks under which an offset is required, highlighting the importance of explicitly stating biodiversity targets in the planning stage (Maron et al. 2018).

Third, although large offsets may have multiple benefits, our results demonstrate that more habitat does not necessarily translate into equal gains in persistence for all species. The implications of not accounting directly for species population dynamics and landscape structures may outweigh benefits delivered by producing large areas of suitable habitat (Figure 5). Where data is available, abundance and demographic variables should be included in offset calculations to ensure populations are tracked and development impacts on populations are accountable. Finally, our results show that benefits delivered by offsets are nuanced and species-specific. Therefore, impacts of metric choice should also be assessed for multiple species simultaneously to determine how these metrics align with achieving several persistence targets. These improvements may go some way towards mitigating development impacts on biodiversity and ensuring long-term conservation benefits.

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